Chapter 14

# FAUNA OF THE EUROPEAN TEMPERATE DECIDUOUS FOREST

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## INTRODUCTION

In the following survey I give a general account of the animal fauna in European deciduous forests, focusing on species spectrum, density and biomass of invertebrates. I will centre upon four well-studied forest ecosystems: a beech-wood on limestone (Göttinger Wald, West Germany), a beech-wood on acid soil (Solling, West Germany), a mull beech-wood in Denmark (Hestehaven) and a mixed deciduous forest in Great Britain (Wytham Wood including Brogden's Belt).

For temperate deciduous forests it is important to recognize that the soils may be classified according to a continuum lying between mull[1] and mor[1]. The Göttingen and Solling areas in Germany are about 50 km apart and provide a good opportunity to compare forests on mull[1] and moder[1] soils, another theme of this chapter.

## WELL-STUDIED EUROPEAN DECIDUOUS FORESTS

### Characterization of habitats

#### Beech forest (Göttingen, West Germany)

The beech forest Göttinger Wald (abbreviated GÖ) is situated in southern Niedersachsen (West Germany) on a plateau of Muschelkalk with an elevation of about 420 m above sea level. The beech forest (Fig. 14.1) about 8 km east of Göttingen is approximately 100 to 115 years old and had a rather uniform canopy layer consisting almost exclusively of beech (*Fagus sylvatica*) trees, which form a dense crown layer. Some trees of other species are interspersed: mostly ash (*Fraxinus excelsior*), and maple (*Acer platanoides*), more rarely *A. pseudoplatanus*, *Quercus robur*, *Q. petraea* and *Ulmus scabra*. A shrub layer is not developed, though in gaps there is a higher growth of young *F. excelsior* trees. The herb layer is, with few exceptions, dense and diverse. Dominant spring geophytes are *Allium ursinum* and *Anemone nemorosa*; additional dominant herbs are *Asarum europaeum*, *Galium odoratum*, *Hordelymus europaeus*, *Lamiastrum galeobdolon*, *Mercurialis perennis*, *Oxalis acetosella* and *Primula elatior*. The forest belongs to the *Melico-Fagetum hordelymetosum* (Dierschke and Song, 1982; here further details are given). The soil is shallow and consists of "terra fusca–rendzina" (about 50%), rendzina (about 26%), terra fusca (about 14%), and some other modifications, containing brown earth (R. Mayer, pers. comm., 1986). The pH ranges from 4.3 to 6.8 (R. Aldag, pers. comm., 1986). Annual precipitation was 1252 mm for 1981, 550 mm for 1982, 635 mm for 1983 (K.-J. Meives, pers. comm., 1986). Further details are given by Hövemeyer (1985).

The fauna has been sampled on two study areas with different methods (cf. Schaefer, 1982): extraction of soil and litter samples with a Kempson bowl extractor (modified by Schauermann) for the macrofauna; extraction with a Macfadyen high-gradient canister apparatus for the mesofauna; extraction with an O'Connor wet extractor for the semiaquatic fauna; sampling with pitfall traps, ground photo-eclectors (emergence traps; see Southwood, 1978) and arboreal photo-eclectors (traps catching animals moving upwards on the tree trunk, cf. Funke, 1971).

[1]"Mull", "mor" and "moder" are explained on p. 517.

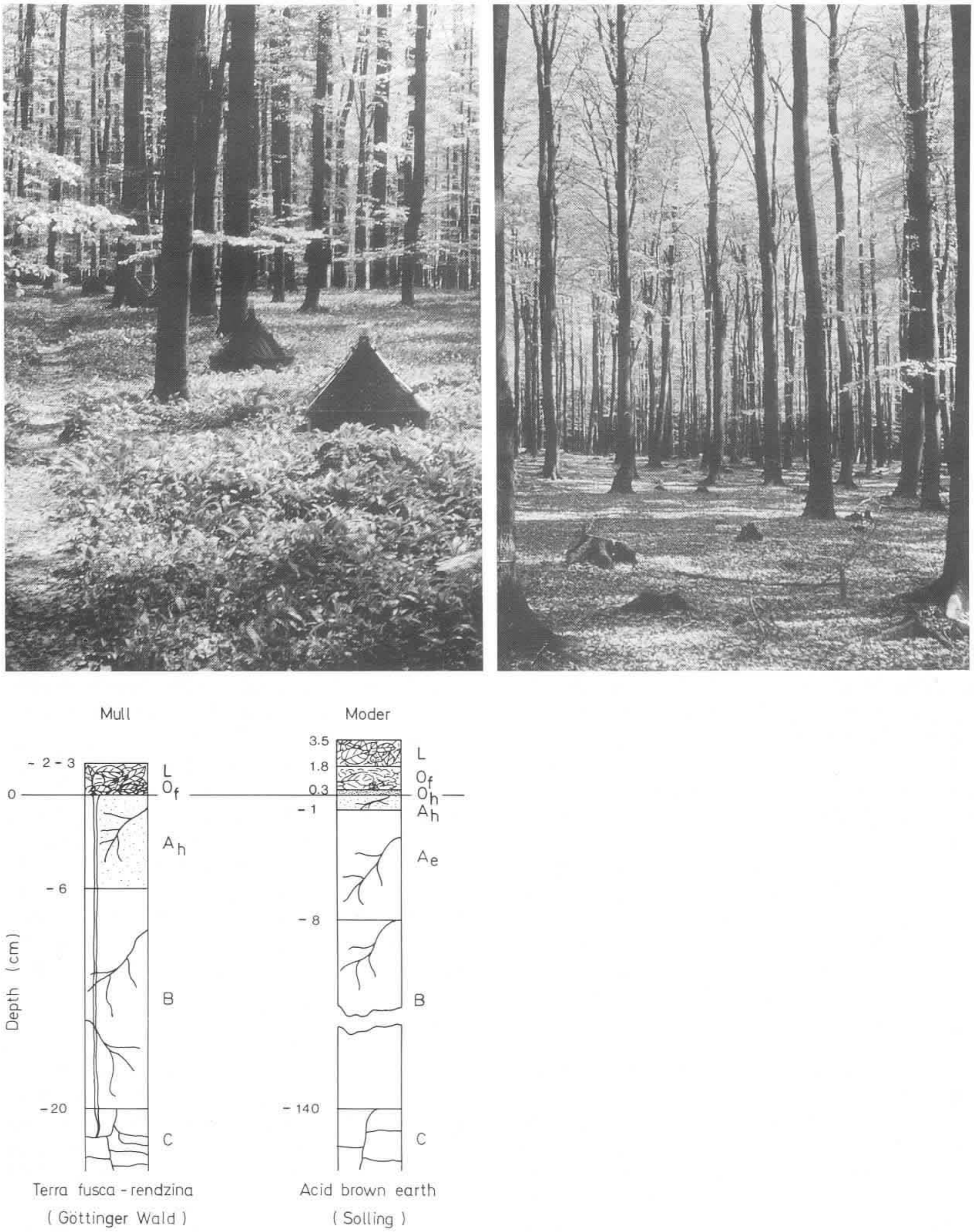


Fig. 14.1. The beech forests Göttinger Wald and Solling (West Germany) with a typical aspect of the wood (top) and a diagrammatic representation of the soil profile (bottom).

**Beech forest (Solling, West Germany)**

This forest (abbreviated SO) is located on the plateau of the Solling, a mountain range of medium altitude about 55 km northwest of Göttingen (southern Niedersachsen). It is a pure beech (*Fagus sylvatica*) stand (Fig. 14.1) without a shrub and herb layer and can be classified as a *Luzulo-Fagetum* (Ellenberg, 1971). Parent material of this acidophilous forest is a loess earth of 40 to 60 cm thickness above a paraautochthonic earth consisting of loamy weathered Buntsandstein material. The unweathered Buntsandstein of Triassic age begins at depths of about 100 cm. The soil is an acid brown earth with a moder form of humus. Values of pH range from about 3 to 4. Annual precipitation is 1063 mm. Further details are given in DeAngelis et al. (1981) and Ellenberg et al. (1986).

**Beech forest (Hestehaven, Denmark)**

The study site is a beech (*Fagus sylvatica*) stand (abbreviated HE) in the mixed forest Hestehaven near Rönde, 25 km north-northwest of Århus, eastern Jutland, Denmark. The age of reproductive overstorey trees is 90 years with an average height of 30 m. An understorey of beech trees and a ground flora are present. Beech and ash (*Fraxinus excelsior*) seedlings occur among the ground flora. The herb layer is diverse. Predominant plants are *Anemone nemorosa*, *Carex sylvatica*, *Circaea lutetiana*, *Ficaria verna*, *Galium odoratum*, *Hordelymus europaeus*, *Melica uniflora* and *Veronica montana* (Hughes, 1975; Nielsen, 1977). The soil is a grey–brown podzol ("Parabraunerde") resting on moraine material deposited during the Würm glaciation. The surface soil is a mull and the subsoil is more or less clayey. The pH ranges from 6 to 7. The litter horizon is rather sharply separated from the surface soil (Nielsen, 1977). Further details appear in DeAngelis et al. (1981).

**Mixed deciduous forest (Wytham Wood, Great Britain)**

Brogden's Belt (abbreviated WY) was used by Phillipson and co-workers for a series of studies of the soil fauna. It is a narrow belt of beech mixed with some other trees. This belt lies towards the centre of Wytham Estate (Oxfordshire, Great Britain) at an altitude of 150 m, and is located on the perimeter of Wytham Great Wood, a mixed woodland of *Acer pseudoplatanus* (sycamore), *Betula pendula* (birch), *Carpinus betulus* (hornbeam), *Castanea sativa* (sweet chestnut), *Fraxinus excelsior* (ash) and *Quercus robur* (oak) as well as *Fagus sylvatica* (beech). Brogden's Belt was planted between 1814 and 1827 and is situated on a raised tropical fringing reef of Jurassic limestone ("Coral rag") of the Upper Corallian beds. The ground flora is sparse and its general distribution reflects those gaps in the canopy which persist longest during early spring (Phillipson et al., 1976). The rendzina-type soil is shallow (6–42 cm in depth) and has a range of pH from 7.3 to 8.0.

The other I.B.P. woodland sites mentioned in the following text are listed and described by DeAngelis et al. (1981). In the I.B.P. woodland stands there is an almost universal predominance of members of the Fagaceae, with oak (*Quercus*) or beech (*Fagus*) or both (Burgess, 1981).

## Fauna

### Protozoa

Four main groups of Protozoa occur in the soil: Flagellata, the poorly studied naked Amoebae, testate Amoebae (Thecamoebae) and Ciliata.

In GÖ the Thecamoebae had a density of 17 to $48 \times 10^6$ ind m$^{-2}$ (biomass 0.4–1.4 g fresh wt m$^{-2}$) with peaks in spring and autumn. The number of species exceeded 65. The abundance of naked Amoebae ranged from 0.5 to $3 \times 10^9$ ind m$^{-2}$; the peak corresponded to a biomass of 11 g dry wt m$^{-2}$. The Zooflagellata had peaks of abundance of $11 \times 10^9$ ind m$^{-2}$ (Meisterfeld, 1986). In SO the mean densities of testate Amoebae were $84.2 \times 10^6$ and $105.7 \times 10^6$ ind m$^{-2}$ in two beech plots (corresponding biomass 1.5 and 2.3 g fresh wt) with maximum value in the $O_f$ layer[1] (Meisterfeld, 1980).

Volz (1964) found testacean densities in a German woodland mull soil of 13 to $19 \times 10^6$ and in a woodland moder soil of 484 to $491 \times 10^6$ ind m$^{-2}$. Volz (1951) estimated a biomass of 658 mg fresh wt of Testacea m$^{-2}$ in a beech mor soil and 427 mg fresh wt m$^{-2}$ in an oak mull. The most extensive study was made by Persson et al. (1980)

[1]For explanation of $O_f$ and other symbols used for litter and soil horizons, see p. 517.

in a Swedish Scots pine (*Pinus sylvestris*) forest. Their density and biomass estimates were $40 \times 10^6$ ind $m^{-2}$ (16 mg dry wt $m^{-2}$) for Flagellata, $86 \times 10^6$ ind $m^{-2}$ (69 mg dry wt $m^{-2}$) for Rhizopoda and $3 \times 10^6$ ind $m^{-2}$ (5 mg dry wt $m^{-2}$) for Ciliata. Thus there are striking differences in density and biomass of testacean populations on mull, moder and mor soils. Stout (1965; quoted from Stout and Heal, 1967) stated that naked Amoebae, flagellates and ciliates generally favour mull soils, which exhibit rapid nutrient turnover, whereas testaceans favour mor soils.

**Nematoda**

The range of density values for Nematoda in temperate deciduous forests is given by Petersen and Luxton (1982), who calculated a median biomass value of 330 mg dry wt $m^{-2}$.

In GÖ, U. Heitkamp (pers. comm., 1986) found a mean density of Nematoda of about $6.4 \times 10^5$ ind $m^{-2}$ with a minimum in June and a maximum in November. About 80% of the population occurred in the upper 9 cm of the soil. In HE, Yeates (1972) found a mean number of $1.1 \times 10^6$ ind $m^{-2}$ and biomass of 0.28 g $m^{-2}$ (as wet mass; 0.17 g $m^{-2}$ as dry mass) up to a soil depth of 6 cm. Over 75 nematode species occurred. In WY, Phillipson et al. (1977) found the mean annual population density of nematodes in the litter and upper 6 cm of the soil to be $0.3 \times 10^5$ ind $m^{-2}$, with a mean biomass of 74.6 mg fresh wt $m^{-2}$. Total numbers revealed a general picture of low densities in spring and high ones in early winter, whereas biomass per square metre was low in late summer–autumn and high in winter. In a beech forest of the Western Carpathians, mean abundance of nematodes was $1.06 \times 10^6$ ind $m^{-2}$ with a mean biomass of 470.4 mg fresh wt $m^{-2}$ for a period of six months (Popovici, 1984). Popovici counted 101 species.

According to Petersen and Luxton (1982), densities, total biomass and individual weights of nematodes are lower in temperate coniferous forests than in deciduous woodlands. A Dutch oak forest (Meerdink) on mor soil corresponds more closely to coniferous forests than to other deciduous forests.

**Other semiaquatic groups**

Data on the other semiaquatic groups (Turbellaria, Rotatoria, Tardigrada and Copepoda) are scarce. V. Büttner (pers. comm., 1986) studied these groups in GÖ, and gave the following values: for species number, mean annual density and mean annual biomass:

| | Species number | Mean annual density (ind $m^{-2}$) | Mean annual biomass (mg dry wt $m^{-2}$) |
|---|---|---|---|
| Turbellaria | 3 | 859 | 48 |
| Rotatoria | 13 | 4893 | 24 |
| Tardigrada | 4 | 4207 | 15 |
| Harpacticida | – | 3873 | 9 |

The rotifers had a maximum in late winter and spring, a minimum in November and December. In SO the density of Turbellaria through summer and autumn had a mean of 1882 ind $m^{-2}$ with a mean biomass of 4 mg dry wt $m^{-2}$ (Schauermann, 1986). The beech-wood HE seems to support relatively small tardigrade populations (Hallas and Yeates, 1972), with a mean density of 4000 ind $m^{-2}$ and an average biomass of 5.4 mg fresh wt $m^{-2}$.

**Gastropoda**

There are comparatively few studies on snails and slugs in temperate deciduous forests. Petersen and Luxton (1982) present a typical biomass value of 270 mg dry wt $m^{-2}$. A low number of gastropods are generally found on moder and mor sites.

In GÖ, Corsmann (1981) found 30 species of Gastropoda: the dominant ones are listed in Table 14.1. Mean annual density amounted to 122 ind $m^{-2}$, mean annual biomass in ash-free dry weight 428 mg $m^{-2}$. In SO, only a few slug species and no snail species occur. Their density and biomass are negligible (Schauermann, 1986). The biomass of 270 mg dry wt $m^{-2}$ reported for HE only represents the large slug *Arion ater* (Jensen, 1975). Four species of slugs occur in WY, but only a single species, *Arion hortensis*, dominated in terms of numbers and biomass (Phillipson, 1983b). Mean annual density of all slugs was 34 ind $m^{-2}$, while mean biomass equalled 266 mg dry wt $m^{-2}$. Snail density was 645 ind $m^{-2}$, and the annual mean ash-free dry weight was 176 mg $m^{-2}$ (Phillipson and Abel, 1983). These authors listed 16 snail species for Brogden's Belt. Jennings and Barkham

TABLE 14.1

Abundance and biomass of important snails and slugs (Gastropoda) in a beech-wood on limestone (Göttinger Wald). Collected by hand (modified from Corsmann, 1981)

| Species | Mean annual abundance (ind $m^{-2}$) | Mean annual biomass (mg ash-free dry wt $m^{-2}$) |
|---|---|---|
| *Aegopinella nitidula* (Draparnaud) | 16.7 | 45.35 |
| *A. pura* (Alder) | 24.0 | 18.00 |
| *Arianta arbustorum* (L.) | 1.1 | 43.53 |
| *Arion ater* (L.)[a] | 0.15 | 0.56 |
| *A. circumscriptus* (Johnston) | 2.2 | 29.04 |
| *Carychium tridentatum* (Risso) | 24.4 | 1.86 |
| *Cochlodina laminata* (Montagu) | 1.5 | 12.93 |
| *Helicodonta obvoluta* (O.F. Müller) | 2.2 | 30.14 |
| *Laciniaria biplicata* (Montagu) | 1.2 | 8.92 |
| *Oxychilus cellarius* (O.F. Müller) | 3.3 | 18.77 |
| *Perforatella incarnata* (O.F. Müller) | 12.7 | 153.55 |
| *Punctum pygmaeum* (Draparnaud) | 1.5 | 0.13 |
| *Trichia hispida* (L.) | 8.8 | 30.27 |
| *Vitrea crystallina* (O.F. Müller) | 16.8 | 5.87 |
| Total (including further species) | 122.2 | 428.4 |

[a]Underestimated by the sampling method.

(1975) estimated mean densities of 18, 19 and 35 ind $m^{-2}$ for slug populations in different areas of an English mixed deciduous woodland. Mason (1970) observed a density of snails in an English deciduous forest of 490 ind $m^{-2}$ and a mean biomass value of 278 mg dry wt $m^{-2}$. Cameron (1982) found values of 37 ind $m^{-2}$ and 175 mg $m^{-2}$, in ash-free dry weight for the snail community of an English deciduous forest on moderately rich soil.

### Enchytraeidae

Synopses of the enchytraeid fauna in temperate deciduous forests were given by Petersen and Luxton (1982), who calculated a mean biomass of 430 mg dry wt $m^{-2}$, and by Axelsson et al. (1984), who gave a range of biomass for northwestern European deciduous forests of 100 to 1640 mg dry wt $m^{-2}$.

In GÖ, Mellin (Mellin, 1982; and pers. comm., 1986) found 35 enchytraeid species with a mean abundance of 20 200 ind $m^{-2}$ and a mean biomass of 0.7 g dry wt $m^{-2}$; 63% of the individuals populated the upper 6 cm of the soil. Peaks of abundance were recorded in March–April, June, August and December. In SO, corresponding values were 134 000 ind $m^{-2}$ and 2688 mg dry wt $m^{-2}$ (Schauermann, 1986). In WY, Phillipson et al. (1979) found the mean annual population density of enchytraeids in the litter and upper 6 cm of the soil to be 14 590 ind $m^{-2}$, with a mean biomass of 1.908 g wet wt $m^{-2}$. Total numbers and biomass had high values in late autumn and winter.

There is a drastic difference between the enchytraeid populations in the moder soil of SO and the mull soil of GÖ, the former being characterized by higher density and biomass, and lower mean body weight (0.0152 mg in SO, 0.035 mg in GÖ), but a lower species diversity. According to Petersen and Luxton (1982), Enchytraeidae are favoured by continuously high levels of soil moisture. Therefore these authors found no clear separation between the density values obtained from mineral mull soils and mor soils with accumulated organic matter. However, the highest enchytraeid numbers reported occur in organic soils. The mixed oak wood at Meerdink (Netherlands) with mor soil has an enchytraeid biomass which compares with the highest biomass values recorded for coniferous forests. At least in some moder or mor sites (such as in SO), average individual weights are comparatively low. Comparisons are rendered more difficult because the densities of enchytraeids for a given habitat seem to decrease from England

through Denmark to Fennoscandia (Abrahamsen, 1972), probably reflecting the different climates (Axelsson et al., 1984).

**Lumbricidae**

Recent summaries on earthworm faunas of temperate deciduous forests are given by Satchell (1983), Zicsi (1983) and Axelsson et al. (1984). Petersen and Luxton (1982) stated that typical biomass estimates for large Oligochaeta (with empty gut) are 200 mg dry wt $m^{-2}$ for mor soils and 5300 mg dry wt $m^{-2}$ for mull soils, which emphasizes the striking difference in earthworm populations in mull and mor soils. A very high biomass value (26 g dry wt $m^{-2}$) has been recorded by Bouché (1975) for a French hornbeam (*Carpinus betulus*) forest on fertile mull at Brunoy.

In GÖ with mull soil, ten earthworm species occur (K. Poser, pers. comm., 1986; Judas et al., 1989). Their abundance and biomass are presented in Table 14.2. The more dominant species are typical forest inhabitants. In SO with moder soil, almost no earthworms occur (Schauermann, 1986). Mean body size is 25 mg dry wt; in comparison, mean body weight of the GÖ population is 41.7 mg dry wt. Phillipson et al. (1976, 1978) studied the lumbricid fauna of WY. They found ten species (*A. caliginosa* was numerically most abundant) with a mean annual density of 164.6 ind $m^{-2}$ for 1971/72 and 117.5 ind $m^{-2}$ for 1972/73. Mean biomass values (preserved wet weight) were 41.0 g and 38.6 g $m^{-2}$.

Petersen and Luxton (1982) stated that fertile mull soils of the temperate region have higher numbers of earthworms, with a high proportion of large anecic and endogaeous[1] species, whereas moder or mor soils, with insignificant earthworm populations, have small epigaeous species, such as the acid-tolerant *Dendrobaena octaedra* and *Lumbricus rubellus* (Wallwork, 1970). The data show clearly the generally higher earthworm biomasses in soils without an organic top horizon, including the typical mull soils of temperate forests. This distinction between earthworm populations in mull and mor (or moder) forest soils is also demonstrated by an analysis by Phillipson et al. (1978).

**Araneida**

Petersen and Luxton (1982) quote only a few studies on the spider fauna of temperate deciduous forests, and give a mean biomass value of 40 mg dry wt $m^{-2}$.

The spider fauna of GÖ is very diverse, and comprises 102 species (Stippich, 1986). Some details are given in Table 14.3. The mean density in the soil–litter subsystem was 166 ind $m^{-2}$, the mean biomass 135 mg dry wt $m^{-2}$. For the SO,

[1]For characterization of the life forms of earthworms see p. 58.

TABLE 14.2

Abundance and biomass of earthworms (Lumbricidae) in a beech forest on limestone (Göttinger Wald). All species are listed. Biomass values exclude gut contents (data from K. Poser, pers. comm., 1986)

| Species | Mean annual abundance (ind $m^{-2}$) | | Mean annual biomass (g ash-free dry wt $m^{-2}$) |
|---|---|---|---|
| | a[a] | b[b] | a[a] |
| *Aporrectodea caliginosa* (Savigny) | 31.11 | 14.0 | 1.37 |
| *A. rosea* (Savigny) | 17.95 | ? | 0.31 |
| *Dendrobaena octaedra* (Savigny) | | 74.61 | |
| *D. pygmaea* (Savigny) | | ? | |
| *Dendrodrilus rubidus tenuis* (Eisen) | (only tree stumps) | | |
| *Lumbricus castaneus* (Savigny) | 25.67 | 55.22 | 0.28 |
| *L. rubellus* (Hoffmeister) | 2.93 | ? | 0.08 |
| *L. terrestris* (L.) | 18.75 | ? | 6.43 |
| *Octolasion cyaneum* (Savigny) | 14.73 | ? | 1.04 |
| *O. lacteum* (Savigny) | 39.02 | 63.81 | 0.75 |
| Total | 154.72 | >239.15 | 9.75 |

[a]a = collecting by hand and formalin method; [b]b = Kempson extraction.

TABLE 14.3

Abundance and biomass of important spiders (Araneida) in a beech-wood on limestone (Göttinger Wald) (data from G. Stippich, pers. comm., 1986)

| Species (adults) | Ke[a] | Pi[a] | Ec[a] | ArEc[a] | Mean annual abundance (ind $m^{-2}$) | Mean annual biomass (mg dry wt $m^{-2}$) |
|---|---|---|---|---|---|---|
| Amaurobidae | | | | | | |
| *Amaurobius claustrarius* (Hahn) | 2 | 11 | 26 | | | |
| *A. fenestralis* (Stroem) | | 1 | 4 | 53 | | |
| Clubionidae | | | | | | |
| *Clubiona terrestris* (Westring) | 3 | 3 | 14 | | | |
| Salticidae | | | | | | |
| *Neon reticulatus* (Blackwall) | 2 | | 39 | | | |
| Agelenidae | | | | | | |
| *Coelotes inermis* (C.L. Koch) | | 11 | 13 | | | |
| *C. terrestris* (Wider) | 2 | 105 | 81 | 14 | | |
| *Histopona torpida* (C.L. Koch) | 5 | 140 | 53 | | | |
| Linyphiidae | | | | | | |
| *Diplocephalus picinus* (Blackwall) | 2 | 3 | 21 | 1 | | |
| *Drapetisca socialis* (Sundevall) | 1 | | 6 | 72 | | |
| *Gonatium rubellum* (Blackwall) | 3 | 12 | 38 | 33 | | |
| *Helophora insignis* (Blackwall) | 2 | | 61 | 1 | | |
| *Lepthyphantes pallidus* (O.P.-Cambridge) | 3 | 9 | 7 | 1 | | |
| *L. tenebricola* (Wider) | 4 | 2 | 18 | | | |
| *L. zimmermanni* (Bertkau) | 8 | 28 | 67 | 6 | | |
| *Linyphia hortensis* (Sundevall) | 3 | 6 | 15 | 7 | | |
| *L. triangularis* (Clerck) | 1 | 1 | 92 | 87 | | |
| *Macrargus rufus* (Wider) | 5 | 7 | 48 | | | |
| *M. herbigradus* (Blackwall) | 45 | 38 | 98 | 1 | 3.5 | 0.76 |
| *Microneta viaria* (Blackwall) | 6 | 4 | 11 | | | |
| *Saloca diceros* (O.P.-Cambridge) | 69 | 47 | 94 | | 5.3 | 0.58 |
| *Walckenaera cucullata* (C.L. Koch) | 2 | 16 | 19 | | | |
| *W. cuspidata* (Blackwall) | 7 | 34 | 116 | 29 | | |
| Total | | | | | 166[b] | 135[b] |

[a]Total number of adult individuals is given sampled during one year by different methods: Ke = Kempson extraction of 12 monthly litter and soil samples (diameter 21 cm); Pi = catches with 6 pitfall traps (diameter 6 cm); Ec = samples with 12 photo-eclectors covering 1 $m^2$ each; ArEc = sampling with one arboreal eclector.
[b]Including juveniles.

Albert (1982) observed a mean density of 462 ind $m^{-2}$ and a mean biomass of 173 mg dry wt $m^{-2}$ (according to a synopsis by Schauermann, 1986). The dominant spiders were *Coelotes terrestris* (mean biomass of 83 mg dry wt $m^{-2}$), *Drapetisca socialis* and *Tapinocyba pallens*. Axelsson et al. (1984) found comparative values for mean annual density and biomass of spiders in a Swedish deciduous forest (Andersby): 220 ind $m^{-2}$, 110 mg dry wt $m^{-2}$.

### Pseudoscorpionida

Pseudoscorpions rarely reach high population densities in European deciduous forests. One of the highest values reported is 105 mg dry wt $m^{-2}$ (mean annual biomass) in Meathop Wood (Great Britain) (Petersen and Luxton, 1982).

In GÖ, three pseudoscorpionid species occur, with *Neobisium muscorum* (Leach) clearly dominating. Total mean annual density in the litter layer was 35 ind $m^{-2}$, mean biomass 16 mg dry wt $m^{-2}$ (Schaefer, 1983b; G. Stippich, pers. comm., 1986). Corresponding values for SO are 89 ind $m^{-2}$, with a mean biomass of 10 mg dry wt $m^{-2}$. Goddard (1976) found three species of pseudoscorpions in an English beech-wood site: *Neobisium muscorum*, *Chthonius orthodactylus* and in low density *Allochernes dubius*. Maximum density of all

species was 97 ind $m^{-2}$, minimum density 4 ind $m^{-2}$.

**Opilionida**

Harvestmen make a minor contribution to the abundance and biomass of the soil–litter fauna (Petersen and Luxton, 1982). However, some species occur in higher vegetation layers, for instance adult *Mitopus morio* and *Platybunus bucephalus* (Bachmann and Schaefer, 1983).

The forest GÖ is inhabited by eight species with a mean annual density of 19 ind $m^{-2}$ and a mean annual biomass of 11 mg dry wt $m^{-2}$ (Table 14.4). Abundance and biomass of Opilionida were extremely low in a Swedish mixed deciduous forest (Andersby): 1.5 ind $m^{-2}$ and 2.0 mg dry wt $m^{-2}$ in the soil–litter subsystem (Axelsson et al., 1984).

**Cryptostigmata (Oribatei)**

A survey of the many studies on cryptostigmatid and other mites in deciduous forests has been given by Petersen and Luxton (1982). Mean annual cryptostigmatid densities are between $100 \times 10^3$ and $300 \times 10^3$ ind $m^{-2}$, and biomasses between 400 and 1000 (typically 700) mg dry wt $m^{-2}$ in temperate forests on mor (or moder) soils; in contrast, woodland on mull soils has smaller populations, ranging between $20 \times 10^3$ and

TABLE 14.4

Abundance and biomass of harvestmen (Opilionida) in a beech-wood on limestone (Göttinger Wald). All species included. Explanation in Table 14.3 (modified from Bachman and Schaefer (1983), including unpublished data)

| Species (juveniles and adults) | Ke[a] | Pi[a] | Ec[a] | ArEc[a] | Mean annual abundance ind $m^{-2}$ | Mean annual biomass mg dry wt $m^{-2}$ |
|---|---|---|---|---|---|---|
| *Anelasmocephalus cambridgei* (Westwood) | 1 | 1 | 1 | | | |
| *Lacinius ephippiatus* (C.L. Koch) | 3 | 13 | 19 | | | |
| *Lophopilio palpinalis* (Herbst) | 93 | 131 | 117 | | 7.15 | 9.8 |
| *Mitopus morio* (F.) | 10 | 34 | 113 | 212 | | |
| *Nemastoma lugubre* (Müller) | | 1 | | | | |
| *Oligolophus tridens* (C.L. Koch) | | 7 | | 1 | | |
| *Platybunus bucephalus* (C.L. Koch) | 3 | 2 | 3 | 3 | | |
| *Trogulus nepaeformis* (Scopoli) | 1 | 8 | 2 | | | |
| Total | | | | | 19 | 11 |

[a]Collection methods: see Table 14.3. The figures are the total number of individuals collected in a year.

TABLE 14.5

Abundance and biomass of important oribatid mites (Cryptostigmata) in a beech-wood on limestone (Göttinger Wald). Extraction of soil and litter samples with the Macfadyen high gradient canister apparatus (data from H.-D. Baaske, pers. comm., 1986)

| Species | Mean annual abundance (ind $m^{-2}$) | Mean annual biomass (mg ash-free dry wt $m^{-2}$) |
|---|---|---|
| *Ceratozetes gracilis* (Michael) | 400 | 6.18 |
| *Chamobates cuspidatus* (Michael) | 560 | 2.33 |
| *Eulohmannia ribagai* (Berlese) | 340 | 2.66 |
| *Hypochthonius rufulus* (C.L. Koch) | 500 | |
| *Nothrus palustris* (C.L. Koch) | 380 | 25.70 |
| *Oppia minus* (Paoli) | 540 | |
| *O. ornata* (Oudemans) | 700 | |
| *O. subpectinata* (Oudemans) | 2220 | 4.03 |
| *Oppiella obsoleta* (Paoli) | 320 | 0.31 |
| *Quadroppia quadricarinata* (Michael) | 1680 | 0.83 |
| *Steganacarus magnus* (Nicolet) | 260 | 42.32 |
| *S. striculus* (C.L. Koch) | 1880 | 19.25 |
| *Suctobelbella forsslundi* (Strenzke) | 840 | |
| Total (including further species and undetermined nymphs) | 16 080 | not calculated |

$50 \times 10^3$ ind $m^{-2}$ and between 100 and 400 (typically 180) mg dry wt $m^{-2}$.

For the GÖ, population data are summarized in Table 14.5. The mean annual density of all Acarina in SO was $355 \times 10^3$ ind $m^{-2}$ with an impressive peak of $1783 \times 10^3$ in late autumn; the mean annual biomass amounted to 2299 mg dry wt $m^{-2}$ (Schauermann, 1986). There are no values available for oribatid mites alone, but this group is the major constituent of the acarine fauna in SO. A thorough analysis of the HE cryptostigmatid fauna was performed by Luxton (1972, 1975, 1981a–e), summarized in Luxton (1982). Annual monthly mean density of the 66 oribatid species was 34 512 in $m^{-2}$, mean biomass 253.3 mg dry wt $m^{-2}$. A main density peak occurred in December coinciding with the peak of litter input and following the peak period of annual rainfall.

The high counts of oribatid mites in the moder soil of SO are in accordance with the general trend that Oribatei are favoured in mor and moder soils of deciduous forests (Petersen and Luxton, 1982). The mean body weight of the SO oribatid mites is higher than that of the GÖ population (with 0.0069 mg dry wt).

**Other Acarina**

Cryptostigmata generally constitute the main component of the soil acarine populations, especially when biomass is considered (Petersen and Luxton, 1982). According to these authors, population density of Astigmata is generally low, Mesostigmata constitute a few percent to about 20% of Acarina, and the percentage of Prostigmata varies from 10 to 30%. The study of Luxton (1982) reported the relative proportion (%) of the soil mite orders in HE, calculated from the values of annual monthly mean density or biomass:

| | Density | Biomass |
|---|---|---|
| Cryptostigmata | 51.1 | 63.1 |
| Prostigmata | 30.4 | 0.9 |
| Mesostigmata | 15.1 | 34.8 |
| Astigmata | 3.3 | 1.2 |

The **Mesostigmata** contain the two trophically different groups Uropodina as microphytophages and Gamasina as zoophages. These should be considered separately (Petersen and Luxton, 1982). In GÖ, 67 species of Gamasina and 11 species of Uropodina occur (E. Schulz, pers. comm., 1986). Dominant mesostigmatid mites are *Cilliba cassidea*, *Pergamasus lapponicus*, *Trachytes aegrota*, *T. pauperior* and *Veigeia nemorensis*. Mean annual density of Uropodina was $3.4 \times 10^3$ ind $m^{-2}$ (biomass 26 mg dry wt $m^{-2}$), mean annual density of Gamasina was $2.6 \times 10^3$ ind $m^{-2}$ (biomass 45 mg dry wt $m^{-2}$) (E. Schulz, pers. comm., 1986). In SO, the Gamasina have a mean annual density of $10.8 \times 10^3$ ind $m^{-2}$ and a biomass of 397 mg dry wt $m^{-2}$ (17.3% of total acarine dry weight) (Schauermann, 1986). Luxton (1982) gave the data for HE as: 66 species, 10.2 ind $m^{-2}$ and 140 mg dry wt $m^{-2}$.

Densities of **Prostigmata** in deciduous forests lie between $7 \times 10^3$ and $15 \times 10^3$ ind $m^{-2}$, with a typical biomass estimate of 10 mg dry wt $m^{-2}$ (Petersen and Luxton, 1982). In HE, annual mean density of prostigmatid mites reached $20.5 \times 10^3$ ind $m^{-2}$ (biomass 3.7 mg dry wt $m^{-2}$). Dominant among the 40 species were *Eupodes* spp., *Microtydeus* sp., *Nanorchestes arboriger* and *Tarsonemus* sp. (Luxton, 1981g, 1982).

**Astigmata** in temperate deciduous forests contain only a few species. In HE, apart from the dominant *Rhizoglyphus echinopus*, only two additional species occurred (Luxton, 1981f, 1982). Mean annual density of all these species was 2250 ind $m^{-2}$, biomass 4.8 mg dry wt $m^{-2}$.

**Isopoda**

The dominant species in temperate deciduous forests belong to the genus *Trichoniscus* (Petersen and Luxton, 1982). In GÖ, the mean annual density of *Trichoniscus pusillus*, the dominant species, was 207 ind $m^{-2}$, and biomass was 36 mg dry wt $m^{-2}$ (Schaefer, 1982; R. Strüve-Kusenberg, pers. comm., 1986). Further species with considerably lower biomass values are *Oniscus asellus* and in moist places *Ligidium hypnorum*. In SO isopods do not occur. The annual mean biomass for HE is 164 mg dry wt $m^{-2}$, for the English forest Meathop Wood, 105 mg dry wt $m^{-2}$. In WY, numbers of *T. pusillus* averaged 480 to 500 ind $m^{-2}$ (biomass 94–98 mg dry wt $m^{-2}$) (Phillipson, 1983a). In the Swedish Andersby forest Isopoda had very low numbers (2.6 ind $m^{-2}$) and biomass (8.5 mg dry wt $m^{-2}$) (Axelsson et al., 1984).

According to Petersen and Luxton (1982) den-

sity of oniscoid Isopoda may be quite high in temperate deciduous forests on mull soils, whereas information on a few mor soils indicates negligible population size.

### Chilopoda

Centipedes are an important group of the predatory macrofauna in the soil–litter subsystem. In most temperate forests they represent more than 20% of the total macrocarnivores (Albert, 1980). Petersen and Luxton (1982) presented a mean estimate of 130 mg dry wt $m^{-2}$ for temperate deciduous forests; however, they emphasized that high values around 1000 mg dry wt $m^{-2}$ may occur.

In GÖ, chilopods reach high density and biomass values (Table 14.6). In SO, the mean annual density was 74 ind $m^{-2}$, and mean biomass was 155 mg dry wt $m^{-2}$. The two dominant species in this forest are *Lithobius curtipes* and *L. mutabilis* (Albert, 1980; Schauermann, 1986). In the Swedish forest Andersby, chilopods were less important than spiders and had a mean annual density of 14 ind $m^{-2}$, a mean biomass of 24 mg dry wt $m^{-2}$ (Axelsson et al., 1984).

### Diplopoda

A typical biomass estimate for the diplopod fauna of temperate deciduous forests is 420 mg dry wt $m^{-2}$. (Petersen and Luxton, 1982). Bornebusch (1930) reported high values of 3.4 and 2.1 g dry wt $m^{-2}$, for a Danish beech-wood and oak-wood respectively.

In GÖ, eight diplopod species occur with a mean annual density of 89 ind $m^{-2}$ and a biomass of about 600 mg dry wt $m^{-2}$. (Schaefer, 1982; Sprengel, 1986, and pers. comm., 1986). *Mycogona germanicum* had the highest density (48 ind $m^{-2}$, 112 mg dry wt $m^{-2}$). Two *Glomeris* species reached high biomass values: *G. marginata* 285 mg; and *G. conspersa* Koch 125 mg dry wt $m^{-2}$. In SO, diplopods are almost completely absent (Schauermann, 1986). Phillipson and Meyer (1984) reported low densities for WY, with a mean value of 7.4 ind $m^{-2}$ and a corresponding biomass of 212 mg fresh wt $m^{-2}$ *Glomeris marginata* was by far the dominant species. In the Swedish forest Andersby the abundance value was very low (0.9 ind $m^{-2}$; 39 mg dry wt $m^{-2}$) (Axelsson et al., 1984).

### Collembola

Mean annual densities between 40 and $70 \times 10^3$ ind $m^{-2}$ seem to be typical for collembolan populations in temperate deciduous forests according to Petersen and Luxton (1982), who gave a median biomass value of 130 mg dry wt $m^{-2}$ for mor soils and 110 mg dry wt $m^{-2}$ for mull soils.

In GÖ, mean annual density of Collembola (comprising 48 species) was $37 \times 10^3$ in 1980, fluctuating from $22 \times 10^3$ to $55 \times 10^3$ ind $m^{-2}$; mean biomass was 153 mg dry wt $m^{-2}$ (Table 14.7) (Wolters, 1983; and pers. comm., 1986). In subsequent years the mean population density changed from $37 \times 10^3$ to $17 \times 10^3$ (1981), $28 \times 10^3$ (1982) and $49 \times 10^3$ ind $m^{-2}$ (1983) (Wolters, 1985). In SO, mean annual density was $63 \times 10^3$ ind $m^{-2}$

TABLE 14.6

Abundance and biomass of centipedes (Chilopoda) in a beech-wood on limestone (Göttinger Wald). Extraction of soil and litter samples with the Kempson apparatus (data from T. Poser, pers. comm., 1986)

| Species | Mean annual abundance (ind $m^{-2}$) | Mean annual biomass (mg ash-free dry wt $m^{-2}$) |
|---|---|---|
| *Brachygeophilus truncorum* (Bergsoe et Meinert) | 31.5 | 6.5 |
| *Geophilus proximus* (C.L. Koch) | 41.8 | 23.3 |
| *Lithobius crassipes* (L. Koch) | 17.0 | 17.6 |
| *L. curtipes* (C.L. Koch) | 5.9 | 7.2 |
| *L. dentatus* (C.L. Koch) | 3.7 | 13.8 |
| *L. macilentus* (L. Koch) | 6.6 | 8.7 |
| *L. mutabilis* (L. Koch) | 43.2 | 121.4 |
| *L. nodulipes* (C.L. Koch) | 5.5 | 6.2 |
| *L. piceus* (L. Koch) | 6.8 | 28.3 |
| *Strigamia acuminata* (Leach) | 24.9 | 32.3 |
| Total | 186.5 | 265.3 |

TABLE 14.7

Abundance and biomass of important springtails (Collembola) in a beech-wood on limestone (Göttinger Wald). Extraction of soil and litter samples with a Macfadyen canister apparatus (modified from Wolters (1983), including new data)

| Family/species | Mean annual abundance (ind $m^{-2}$) | Mean annual biomass (mg ash-free dry wt $m^{-2}$) |
|---|---|---|
| Hypogastruridae | | |
| *Hypogastrura denticulata* (Bagnall) | 1514 | 6.89 |
| others, including Neanuridae | 568 | 2.60 |
| Onychiuridae | | |
| *Tullbergia krausbaueri* Börner | 6435 | 4.44 |
| others | 3803 | 7.81 |
| Isotomidae | | |
| *Folsomia quadrioculata* (Tullberg) | 4164 | 13.17 |
| *Isotomiella minor* (Schäffer) | 8706 | 10.72 |
| others | 265 | 0.86 |
| Entomobryidae | | |
| *Lepidocyrtus lignorum* F. | 3791 | 22.97 |
| *Tomocerus flavescens* (Tullberg) | 568 | 57.06 |
| others | 265 | 8.88 |
| Sminthuridae | | |
| *Dicyrtomina ornata* (Nicolet) | 118 | 0.77 |
| *Megalothorax minimus* (Willem) | 3407 | 2.97 |
| *Sminthurus viridis* L. | 110 | 1.84 |
| others | 340 | 5.10 |
| Total | 37 853 | 153.12 |

with a mean biomass of 246 mg dry wt $m^{-2}$ (Schauermann, 1986). In HE, the population density of springtails varied from $19 \times 10^3$ to $67 \times 10^3$ ind $m^{-2}$ during two years. The biomass varied through one year from 76 to 160 mg dry wt $m^{-2}$. About 60 species were found within the research site (Petersen, 1980). A Swedish mixed deciduous forest (Andersby) was characterized by a mean springtail abundance of $66 \times 10^3$ ind $m^{-2}$ (biomass 106 mg dry wt $m^{-2}$) (Axelsson et al., 1984) and a species number of 37 (Petersen and Luxton, 1982). In general deciduous forests seem to be rich in collembolan species: in Meathop Wood (Great Britain) 43 species were recorded (Hale, in Petersen and Luxton, 1982), and in a forest in Görlitz (East Germany), 38 species (Dunger, 1968).

The soil and litter subsystem of the moder SO beech-wood maintains higher springtail populations than the mull GÖ beech-wood. Mean body weight is almost the same (0.0039 mg dry wt for SO; 0.0040 mg dry wt for GÖ). Petersen and Luxton (1982) state that populations originating from "mesic" soils are on average higher than those from either "wet" or "dry" soils. Soils with an accumulated layer of organic matter have in general shown higher collembolan densities than mineral soils.

**Other soil and litter mesofauna groups**

For **Pauropoda** the only relevant study is by Axelsson et al. (1984), who found a mean abundance of 3800 ind $m^{-2}$ and a biomass of 2.3 mg dry wt $m^{-2}$ in a Swedish mixed deciduous forest (Andersby).

In GÖ, the **Symphyla** had a mean density of 57 ind $m^{-2}$ (T. Sprengel, pers. comm., 1986). Axelsson et al. (1984) gave values of 100 ind $m^{-2}$ and 1.3 mg dry wt $m^{-2}$ for Andersby.

**Diplura** have a low mean annual density of 34 to 317 ind $m^{-2}$ in GÖ (Wolters, 1985). The same is true for SO (277 ind $m^{-2}$: Schauermann, 1986).

Obviously **Protura** play an inferior role in the soil community, too. Mean annual density values for GÖ ranged from 410 to 2354 ind $m^{-2}$ (Wolters, 1985), the value for SO was 278 ind $m^{-2}$ (Schauermann, 1986). Another estimate is that of Healey (1971), who calculated a density of 6500 ind $m^{-2}$ for Protura in a Danish beech-wood. Gunnar-

son (1980) found a density of 3600 ind $m^{-2}$ in a Swedish oak-wood in October.

**Hemimetabolous insects**

There are only few population estimates of Ensifera, Dermaptera, Blattariae, Psocoptera, Thysanoptera and Rhynchota in connection with ecosystem studies. Some quantitative data are given by Nielsen (1975), Axelsson et al. (1984) and Schauermann (1986).

**Ensifera.** A typical species of European deciduous forests is *Meconema thalassinum*, which is abundant in GÖ.

**Dermaptera.** Some authors stress the importance of *Chelidurella acanthopygia* in deciduous forests. The population in SO had a density of 16 ind $m^{-2}$ leaving the ground zone in May (samples with photo-eclectors, Schauermann, 1986), corresponding to a biomass of 112 mg dry wt $m^{-2}$. Axelsson et al. (1984) found mean values of 1.3 ind $m^{-2}$ and 6.0 mg dry wt $m^{-2}$ in the Andersby deciduous forest.

**Psocoptera** are a prominent group in the phloeosphere (see page 66). In GÖ only few species were present on the ground in low density.

**Thysanoptera** occur mainly in the herb layer. Schauermann (1986) recorded a density of 34 ind $m^{-2}$ (biomass 0.3 mg dry wt $m^{-2}$) in May, sampled with photo-eclectors. Corresponding values in GÖ were 28 ind $m^{-2}$ in May and 33 ind $m^{-2}$ from mid-May to mid-June.

**Rhynchota**. Dominant phytophagous and predatory Heteroptera of the canopy layer in GÖ are *Anthocoris confusus*, *Blepharidopterus angulatus*, *Miris striatus*, *Phytocoris dimidiatus* and *P. tiliae*. Typical Auchenorrhyncha are Typhlocybinae (see Chapter 6), with *Fagocyba cruenta* in beech canopy (Nielsen, 1975; Schauermann, 1986). The dominant aphid (Aphidoidea) in beech-forest canopies is *Phyllaphis fagi* with a mean density of $0.52 \times 10^3$ ind $m^{-2}$ (biomass 18 mg dry wt $m^{-2}$) in HE (Russel: in Schauermann, 1986). In beech forests, the beech coccus, *Cryptococcus fagi* (Coccoidea) is a typical inhabitant of tree trunks (Nielsen, 1975).

**Coleoptera**

Dominant families are Carabidae, Staphylinidae, Elateridae and Curculionidae. Most coleopteran species are sampled quantitatively by extracting soil samples and by using photo-eclectors, as was done for SO (Ellenberg et al., 1986; Schauermann, 1986) and GÖ (Schaefer, personal observation). Both GÖ and SO are characterized by high species diversity of beetles (cf. Table 14.12). Total mean density of Coleoptera in the soil–litter subsystem was 991 ind $m^{-2}$ (biomass of 1258 mg

TABLE 14.8

Abundance and biomass of important carabid beetles (Coleoptera) in a beech-wood on limestone (Göttinger Wald) (modified from Martius, 1986)

| Species (adults) | Ke[a] | Pi[a] | Ec[a] | ArEc[a] | Abundance (ind $m^{-2}$) (20 May) | (10 Sept) |
|---|---|---|---|---|---|---|
| *Abax ovalis* (Duftschmid) | 1 | 17 | 4 | | 3 | 1 |
| *A. parallelepipedus* (Piller et Mitterpacher) | 1 | 284 | 15 | | 1 | |
| *Anisodactylus nemorivagus* (Duftschmid) | 2 | 4 | 7 | | | |
| *Carabus auronitens* (F.) | 1 | 22 | 6 | 1 | | |
| *C. coriaceus* (L.) | | 38 | 2 | | | |
| *C. irregularis* (F.) | | 23 | | 11 | 2 | 1 |
| *C. nemoralis* (Müller) | 2 | 69 | 13 | | 1 | 1 |
| *Cychrus caraboides* (L.) | 1 | 3 | | | | |
| *Loricera pilicornis* (F.) | 2 | | 7 | | | |
| *Molops piceus* (Panzer) | | | | | 8 | |
| *Pterostichus melanarius* (Illiger) | | 20 | 16 | | 3 | |
| *P. metallicus* (F.) | | 41 | 15 | | 3 | 2 |
| *P. oblongopunctatus* (F.) | 1 | 3 | 11 | | 3 | 2 |
| Total (including other species) | 9 | 537 | 101 | 13 | 28 | 9 |

[a]Collection methods, see Table 14.3. The figures are the total number of adults collected in a year.

dry wt $m^{-2}$) in SO (Schauermann, 1986), and 350 ind $m^{-2}$ (biomass of 480 mg dry wt $m^{-2}$) in a Swedish deciduous forest (Andersby) (Axelsson et al., 1984). Data for carabid, staphylinid and curculionid beetles in GÖ are given in Tables 14.8 to 14.10. Dominant curculionid beetles in HE were *Phyllobius argentatus* and *Rhynchaenus fagi*, making up 40% of all canopy invertebrates (Nielsen, 1975). Obrtel (1971), using pitfall traps, found 162 species of Coleoptera in a Moravian lowland forest.

### Hymenoptera

Dominant groups are Ichneumonidae, Braconidae, and other parasitoid species (for instance, Chalcidoidea) (Nielsen, 1975), mostly with a high total number of species. Only in some types of deciduous forests are Formicidae present. In GÖ, Ulrich (1987) found 510 species in 28 families. Total abundances ranged from 114 to over 800 ind $m^{-2}$ $yr^{-1}$ within a study period of several years. Species which develop in dipterous larvae were of major importance (170 species; 51 to more than 790 ind $m^{-2}$ $yr^{-1}$), followed by the parasitoids of Coleoptera (39 species; 8–60 ind $m^{-2}$ $yr^{-1}$) and Lepidoptera (71 species; 9–31 ind $m^{-2}$ $yr^{-1}$). About 90 species feed on saprophagous and mycophagous larvae. Other abundant guilds are the parasitoids of gall-makers (43 species) and leaf-miners (49 species). Schauermann (1986) records a density of "Apocrita" in SO in May of 295 ind $m^{-2}$ (biomass 10.2 mg dry wt $m^{-2}$, sampled with photo-eclectors).

### Diptera

Dipteran larvae have high biomass values in the soil–litter subsystem. Petersen and Luxton (1982) give a median value for temperate deciduous forests of 330 mg dry wt $m^{-2}$. Families dominating in biomass and/or density are Cecidomyiidae, Chironomidae, Sciaridae and Tipulidae (Healey and Russel-Smith, 1971; Petersen and Luxton, 1982; Volz, 1983; Axelsson et al., 1984; Hövemeyer, 1984, 1985; Schauermann, 1986).

In GÖ, Hövemeyer (1984, 1985) found 40 dipterous families with more than 245 species. Annual mean larval abundance was 2847 ind $m^{-2}$, annual mean biomass 166.5 mg dry wt $m^{-2}$. The most abundant families were Sciaridae (36.7%), Lestremiidae (20.9%), Chironomidae (14.0%) and Empididae (12.3%). From March to December 1980, 1721 adults $m^{-2}$ (corresponding to 347.8 mg dry wt $m^{-2}$) were trapped in ground photo-eclectors (Table 14.11). In SO, mean annual density of dipterous larvae was 7415 ind $m^{-2}$, mean biomass 628 mg dry wt $m^{-2}$ (Altmüller, 1979; Schauermann, 1986). In a Swedish deciduous forest (Andersby), Axelsson et al. (1984) recorded a mean density of dipteran larvae of 1300 ind $m^{-2}$, and a mean biomass of 130 m dry wt $m^{-2}$. According to Petersen and Luxton (1982), the maximum biomass reported is 1.8 g dry wt $m^{-2}$,

TABLE 14.9

Abundance and biomass of important staphylinid beetles (Coleoptera) in a beech-wood on limestone (Göttinger Wald) (modified from Schaefer, 1983a)

| Species (adults) | Ke[a] | Pi[a] | Ec[a] | ArEc[a] | Mean annual abundance (ind $m^{-2}$) | Mean annual biomass (mg dry wt $m^{-2}$) |
|---|---|---|---|---|---|---|
| *Anthophagus angusticollis* (Mannerheim) | | | 58 | 163 | | |
| *Eusphalerum abdominale* (Gravenhorst) | 2 | | 103 | | | |
| *Leptusa ruficollis* (Erichson) | | 2 | 2 | 112 | | |
| *Ocalea badia* (Erichson) | 5 | 40 | 29 | | 0.4 | 0.1 |
| *Othius myrmecophilus* (Kiesewetter) | 53 | 2 | | | 4.1 | 2.4 |
| *O. punctulatus* (Goeze) | 12 | 15 | 24 | | 0.9 | 5.1 |
| *Philonthus decorus* (Gravenhorst) | 2 | 280 | 113 | | 0.2 | 1.5 |
| *P. fuscipennis* (Mannerheim) | 6 | 4 | 50 | | 0.5 | 3.7 |
| *P. rotundicollis* (Ménétriès) | 3 | | 10 | | 0.2 | 1.6 |
| Total (including further species) | 169 | 398 | 787 | 316 | 26 | 37 |

[a]Collection methods: see Table 14.3. The figures are the total number of adults collected in a year.

TABLE 14.10

Abundance and biomass of important curculionid beetles (Coleoptera) in a beech-wood on limestone (Göttinger Wald) (data from B. Wagner, pers. comm., 1986)

| Species (adults) | Ke[a] | Ec[a] | ArEc[a] | Emerging adults | |
|---|---|---|---|---|---|
| | | | | density ind ($m^{-2}$ $yr^{-1}$) | biomass (mg dry wt $m^{-2}$ $yr^{-1}$) |
| Canopy layer | | | | | |
| *Phyllobius argentatus* (L.) | | 277 | 589 | 8.9 | 20.9 |
| *P. calcaratus* (F.) | | 31 | 129 | 0.8 | 6.8 |
| *Polydrusus mollis* (Ström) | | 24 | 92 | 0.7 | 7.0 |
| *P. pterygomalis* (Boheman) | | 154 | 125 | 7.4 | 14.8 |
| *P. sericeus* (Schaller) | | 80 | 271 | 3.3 | 14.3 |
| *Rhynchaenus fagi* (L.) | | 138 | | | |
| Total (including other species) | | | | ≈22 | ≈64 |
| | | | | | Mean density (ind $m^{-2}$) |
| Herb layer | | | | | |
| *Acalles camelus* (F.) | + | | | | |
| *A. turbatus* (Boheman ?) | + | | | | |
| *Apion pallipes* (Kirby) | 104 | | | | 4.4 |
| *Barynotus moerens* (F.) | 7 | | | | 0.5 |
| *Leiosoma deflexum* (Panzer) | 115 | | | | 8.0 |
| *Sciaphilus asperatus* (Bonsdorff) | + | | | | |
| *Tropiphorus carinatus* (Müller) | 24 | | | | 0.9 |
| Total (including other species) | | | | | ≈13 |

[a]Collection methods: see Table 14.3. The figures are the total number of adults collected in a year. For some species samples concern different years. + =present.

recorded for a Danish beech mor (Bornebusch, 1930).

In SO, density and biomass of dipteran larvae are considerably higher than in the mull soil of GÖ. Mean average individual dry weight of the larvae in GÖ is 0.057 mg, of SO 0.085 mg. Similarly, Petersen and Luxton (1982) observed that the largest biomass values of dipteran larvae within temperate deciduous forests usually are found in acid moder and mor soils.

### Lepidoptera

Lepidoptera are typical inhabitants of the vegetation layers in temperate deciduous forests, as ectophagous larvae as well as leaf-miners.

In GÖ, Winter (1985) found 53 species. Dominant was *Chimabacche fagella*, with a density of emerging adults of 1.4 ind $m^{-2}$. Important beech leaf-miners are *Phyllonorycter maestingella* (=*Lithocolletis faginella*), with a density of emerging adults of 7.0 $m^{-2}$, and *Stigmella hemargyrella* (=*Nepticula basalella*), with 1.9 mines per leaf (Winter, 1985). For SO (with 31 species), Schauermann (1986) gives a mean density of Lepidoptera of 131 ind $m^{-2}$, corresponding to a biomass of 70 mg dry wt $m^{-2}$.

### Other holometabolous insects

Additional typical holometabolous insect groups of European deciduous forests are Planipennia, Mecoptera and Trichoptera (with *Enoicyla pusilla*, living as larvae in the litter: Van der Drift and Witkamp, 1960), apart from parasitic taxa such as Siphonaptera.

**Planipennia**. A typical species of the shrub and canopy layer is *Hemerobius micans*, with a maximum density of almost 1 ind $m^{-2}$ in GÖ. According to Schauermann (1986) the Planipennia have a density of 4 ind $m^{-2}$ in May, when the individuals are leaving the ground zone.

TABLE 14.11

Abundance and biomass of important families of Diptera in a beech-wood on limestone (Göttinger Wald) (modified from Hövemeyer, 1984)

| Families | Larvae[a] mean annual abundance (ind $m^{-2}$) | Larvae[a] mean annual biomass (mg dry wt $m^{-2}$) | Density of emerging adults Ec[b] (ind $m^{-2}$ $yr^{-1}$) | Adults ArEc[b] |
|---|---|---|---|---|
| *Cecidomyiidae* | 30.5 | 4.3 | 661.0 | 1056 |
| *Ceratopogonidae* | 141.8 | 2.6 | 148.7 | 0 |
| *Chironomidae* | 397.6 | 9.5 | 126.8 | 53 |
| *Lestremiidae* | 595.4 | 20.9 | 144.3 | 24 |
| *Limoniidae* | 103.3 | 13.2 | 28.5 | 60 |
| *Sciaridae* | 1045.5 | 28.7 | 303.8 | 22 |
| *Tipulidae* | 11.2 | 11.1 | 1.5 | 174 |
| All *Nematocera* | 2346.1 | 91.1 | 1448.8 | 1473 |
| *Empididae* | 250.3 | 28.8 | 31.3 | 11 |
| *Fanniinae* | 14.7 | 2.7 | 3.0 | 4 |
| *Lauxaniidae* | 71.1 | 2.9 | 17.3 | 11 |
| *Lonchopteridae* | 12.3 | 1.5 | 11.2 | 0 |
| *Phoridae* | 8.4 | 0.3 | 169.7 | 132 |
| *Rhagionidae* | 26.3 | 28.0 | 1.8 | 6 |
| All *Brachycera* | 501.2 | 75.5 | 272.5 | 220 |
| All *Diptera* | 2847.2 | 166.5 | 1721.3 | 1693 |

[a]Soil and litter samples extracted by a flotation method.
[b]Collection methods for adults: see Table 14.3. Last column total collected over one year.

### Aves and Mammalia

Marcuzzi (1979) and Rahmann (1986) give an account of vertebrates in European forests.

In GÖ, the density of breeding songbirds is 2.01 pairs $ha^{-1}$ (M. Corsmann, pers. comm., 1986). Typical dominant species are *Anthus trivialis*, *Erithacus rubecula*, *Fringilla coelebs*, *Parus major*, *Troglodytes troglodytes* and *Turdus merula*. A thorough analysis of the bird fauna in SO was made by Scherner (1977). He found a density of breeding birds of 1.5 pairs $ha^{-1}$ with a biomass of 10 g fresh wt $ha^{-1}$.

Higher densities are attained by small mammal populations. A review is given by Hayward and Phillipson (1979). In GÖ, the following species are present: *Apodemus flavicollis*, *Clethrionomys glareolus*, *Sorex araneus* and *S. minutus* (M. Sayer, pers. comm., 1986).

## COMPARISON OF DECIDUOUS FORESTS ON MULL AND MOR SITES

Table 14.12 serves as a basis for the following comparison between mull and moder soils of European deciduous forests.

There have been numerous attempts to classify forest soil types. The two main extremes are mull and mor (syn. raw humus). In mor soil the current litter (L) lies over a matted layer of partly decomposed material ($O_f$ — the fermentation layer), in which the degree of decomposition increases with depth. The $O_f$ layer grades into a lower horizon, the humus horizon ($O_h$), of well-decomposed organic material, visibly unrecognizable as to plant origin. Normally the $O_h$ horizon shows an abrupt transition to the underlying mineral soil horizon (A). The mor is generally acidic and contains a large amount of organic topsoil material (cf. Fig. 14.1 and Table 14.13).

In the mull soil there is no clear separation between the thin organic layer (O) and the soil. The uppermost soil horizon ($A_h$) is an intimate mixture of well-humified organic matter and mineral soil. A litter layer (L) may be present. However, the current litter may be essentially absent towards the end of the growing season, just before major leaf fall. Individual pieces of partially decomposed organic matter may constitute an ill-defined $O_f$ layer. An $O_h$ horizon is not present. The standing crop of soil organic matter is lower in mull than in

TABLE 14.12

Synopsis of data for invertebrate populations in the beech forests Göttinger Wald (with mull soil) and Solling (with moder soil). – = not studied; 0 = not present. Data from Schaefer (1982) and co-workers for the Göttinger Wald; Schauermann (1986 and pers. comm., 1986) for the Solling. Some minor groups are omitted. A recent synthesis is given by Schaefer and Schauermann (1990)

| Animal group | Göttinger Wald | | | Solling | | |
|---|---|---|---|---|---|---|
| | species numbers | mean annual density ($m^{-2}$) | mean annual biomass (mg dry wt $m^{-2}$) | species numbers | mean annual density ($m^{-2}$) | mean annual biomass (mg dry wt $m^{-2}$) |
| Protozoa | | | | | | |
| *Flagellata* | – | $2.7 \times 10^9$ | 54 | – | – | – |
| *Amoebina* | – | $3.5 \times 10^9$ | 1133 | – | – | – |
| *Testacea* | 65 | $84 \times 10^6$ | 343[b] | 51 | $57 \times 10^6$ | 256 |
| *Ciliata* | – | – | – | – | – | – |
| Turbellaria | 3 | 859 | 8 | 3 | 1882 | 4 |
| Nematoda | 65 | 732 000 | 146 | – | – | – |
| Rotatoria | 13 | 4893 | 5 | – | – | – |
| Mollusca | | | | | | |
| *Gastropoda* | 30 | 120 | 430 | 4 | 0 | 0 |
| Annelida | | | | | | |
| *Enchytraeidae* | 35 | 22 300 | 600 | 15 | 108 000 | 1640 |
| *Lumbricidae* | 11 | 205 | 10 700 | 4 | 19 | 168 |
| Arthropoda | | | | | | |
| *Tardigrada* | 4 | 4207 | 4 | – | 41[c] | 9[c] |
| *Arachnida* | | | | | | |
| *Araneida* | 92 | 166 | 135 | 93 | 462 | 173 |
| *Pseudoscorpionida* | 3 | 35 | 16 | 2 | 89 | 10 |
| *Opilionida* | 8 | 19 | 11 | 4 | 20[e] | 6[e] |
| *Cryptostigmata* | 61 | 25 900 | 180 | 72 | 101 810 | 195 |
| *Gamasina* | 67 | 2620 | 45 | – | 10 800 | 397 |
| *Uropodina* | 11 | 3390 | 26 | – | – | – |
| Crustacea | | | | | | |
| *Harpacticoida* | – | 3873 | 2 | 1 | 3300[c] | 0.6[c] |
| *Isopoda* | 6 | 286 | 93 | 0 | 0 | 0 |
| Myriapoda | | | | | | |
| *Chilopoda* | 10 | 187 | 265 | 7 | 74 | 155 |
| *Diplopoda* | 6 | 55 | 618 | 1 | 0 | 0 |
| *Symphyla* | 2 | 57 | – | 1 | – | – |
| Insecta | | | | | | |
| *Diplura* | – | 146 | – | 1 | 277 | – |
| *Protura* | – | 2354 | – | 1 | 278 | – |
| *Collembola* | 48 | 37 835 | 153 | >11 | 63 000 | 246 |
| *Orthopteroidea* | 2 | – | – | 2 | – | – |
| *Psocoptera* | – | – | – | – | – | – |
| *Thysanoptera* | – | 28–36[d] | – | – | 34[d] | 0.3[d] |
| *Heteroptera* | 19 | 4[g] | – | 14 | 15[e] | 6[e] |
| *Auchenorrhyncha* | 18 | 65[g] | – | 1 | 4[e] | 0.5[e] |
| *Sternorrhyncha* | >8 | – | – | 1 | – | – |
| *Raphidioptera* | – | – | – | 1 | – | – |
| *Planipennia* | >5 | – | – | ≥1 | 4[e] | 3[e] |
| Coleoptera | | | | | | |
| *Carabidae* | 24 | 5 | 144 | 26 | 7 | 93 |
| *Staphylinidae* | 85 | 103 | 76 | 117 | 314 | 180 |
| *Elateridae* | 11 | 37[h] | 104[h] | 4 | 332[h] | 706[h] |
| *Curculionidae* | 34 | >21 | >64 | 12 | 296 | 279 |
| All Coleoptera | 254 | – | – | 225 | 991 | 1258 |
| Hymenoptera | 704 | 125[b] | 18[b] | – | 295[f] | 10.2[f] |
| Lepidoptera | 53 | – | – | 40 | 131 | 70 |
| Diptera | >245[a] | 2706[h] | 119[h] | 40 | 7415[h] | 628[h] |

[a]42 families; [b]emerging adults; [c]single measurement; [d]peak density; [e]in May in the litter–herb layer; [f]Apocrita in May; [g]sum of eclector samples from March to October; [h]larvae.

TABLE 14.13

Characteristics of mull and mor (or moder) soil types of temperate deciduous forests. Some of the data based on Wallwork (1976), Swift et al. (1979) and Petersen and Luxton (1982)

| | Mull | Mor (Moder) |
|---|---|---|
| Horizons | O rarely recognizable, $A_h$ good mixing of organic and mineral material | O well defined, $A_h$ sharp, deep and largely organic |
| Organic matter | Low cellular component, $A_h$ rarely over 10% organic content | High cellular component, $A_h$ has 20–80% organic content |
| pH | 5.0–7.0 (rarely higher) | 3.5–5.0 |
| C:N ratio | Low (<15) | High (>20) |
| Crumb formation | High | Low |
| Ground vegetation | Present | ±absent |
| Microflora | High bacterial density; fungal mycelium less abundant | Low bacterial density; fungal mycelium abundant |
| Microfauna | High abundance | Lower abundance |
| Mesofauna | Low abundance | Higher abundance |
| Macrofauna | High abundance and biomass | Low to very low abundance |
| Total fauna | High biomass | Lower biomass |
| Other correlates of the fauna | Mean body size high; diversity high; vertical distribution to deeper strata more pronounced; in phenology a tendency to minima in winter and summer; fewer fungal and more detritus substrate feeders | Mean body size lower; diversity lower; vertical distribution to deeper strata less pronounced; in phenology no winter and summer depression; more fungal and litter feeders |

mor soils under equilibrium conditions with the same litter input (Swift et al., 1979). There are many other differences (cf. Table 14.13); for instance, in mull soils the structure of organic topsoil is more diverse, and pH and calcium availability are higher. Microflora populations differ also. Acid soils are not favourable for bacterial populations, probably because acid soils limit macro-organisms such as earthworms (Spurr and Barnes, 1980). Under conditions unfavourable to bacterial growth, fungi are better able to survive, grow, and become dominant. More details are given by Wallwork (1970, 1976) and Swift et al. (1979). The formation of either mor or mull (or intermediate types) depends on the type of soil parent material, abiotic soil factors, macroclimate and tree species. Natural hardwoods favour the development of a mull condition, whereas conifers may favour mor. An intermediate type is "moder" with an L–$O_f$–$O_h$ stratification. The $O_f$ layer is not matted as in mor, the $O_h$ layer is quite thin (under 2–3 cm), and the lower portion usually shows a mechanical mixing of organic and mineral particles ($A_h$ horizon). Some authors (such as Petersen and Luxton, 1982) include moder in the category of mor. I will apply the terminology "mull–moder–mor" in the following paragraphs.

For the following comparison, deciduous forests on mull soils (Göttinger Wald GÖ; Wytham Wood WY; Hestehaven HE; and others) are compared with those on moder (Solling SO) or mor soils (Meerdink). Andersby has a mixture of mull and moder soil (Axelsson et al., 1984). Because of the complete faunal analysis that is available (cf. Table 14.12) I will concentrate on SO (Ellenberg et al., 1986; Schauermann, 1986) and GÖ (Schaefer, 1982; and unpublished data).

## Fauna

The following faunal groups exhibit striking differences between GÖ and SO (cf. Table 14.12):

Protozoa, Nematoda, Gastropoda, Enchytraeidae, Lumbricidae, Cryptostigmata, Isopoda, Diplopoda, Collembola, Diptera and some predatory macroarthropod groups (Araneida, Chilopoda and Staphylinidae). In the mull soil many Protozoa (naked Amoebae, flagellates and ciliates), the nematodes, gastropods, lumbricids, isopods, diplopods and chilopods are favoured. The testaceans (Protozoa), enchytraeids, oribatid mites, collembolans, dipterans, araneids and staphylinids, occur with higher population density and/or biomass in the moder soil.

Some suggestions about the different habitat preferences of the fauna are possible. Probably Protozoa and Nematoda utilize the rich bacterial populations in mull soil, and microfaunal populations feeding on fluids depend on rapid nutrient turnover. The reason for the suppression of shell-bearing gastropods appears to be the low calcium availability. This element is a prerequisite for the formation of the shell. Enchytraeids need high moisture (Petersen and Luxton, 1982), which is secured more in moder or mor soils than in mull soils. Density and biomass of Enchytraeidae are inversely related to density and biomass of earthworms, and perhaps are directly influenced by earthworm occurrence. The susceptibility of individuals to low pH values (Piearce, 1972; Edwards and Lofty, 1977) may be one reason for the absence of most earthworm species from acid soils. Furthermore, the habit of substrate feeding is not possible in the A horizon of moder and mor soils. Oribatid mites and collembolans might be favoured in moder or mor soils by the high quality of available food, the fungal biomass. Fungi provide enough calcium, which is accumulated by these microfloral populations (Cromack et al., 1979). Many collembolan species are preferably fungal feeders and may be favoured by high population densities of microfungi (Kilbertus and Vannier, 1979; Swift et al., 1979). A comparison of Tomoceridae of different habitats showed that individuals within a thick organic topsoil layer fed on humus and hyphae, while those living over a soil with sparse litter and organic matter mainly fed on spores and undetermined organic matter (Gilmore and Raffensperger, 1970). The reason for the absence of isopods and diplopods in acidic mull and mor soils may be the low availability of calcium, this element being an important constituent of the skeleton. The voluminous topsoil organic layers in the moder and mor ground floor may favour the establishment of predatory macrofauna populations, such as spiders, carabids and staphylinids (Schaefer, 1983a, 1983b). The chilopods which penetrate deeper into the soil (mainly Geophilomorpha), appear to be favoured by the crumb structure of the $A_h$ horizon in the GÖ mull soil, which is additionally aerated by the activity of earthworms. The availability of lumbricid worms as food may also favour chilopod populations. According to Wallwork (1970), carnivorous arthropods (such as centipedes, spiders, pseudoscorpions, opilionids, and predatory beetles) are generally better represented in mor profiles than in mull, probably parallelling the high numbers of microarthropods as prey.

### Spatial patterns

As a general rule, soil animals in mor sites have a more even vertical distribution (Petersen and Luxton, 1982). However, this uniformity characterizes only the topsoil organic layer, as the mineral A horizon is avoided by many soil animal populations. Even in the moder soil of SO, most of the animal populations are concentrated in the comparatively thin organic layer ($L+O_f+O_h+A_h$). In contrast, the GÖ populations penetrate deeper into the soil, the $A_h$ horizon being much more extensive in the mull than in the moder soil. Deep burrowing and endogaeous earthworms contribute to mixing of organic and inorganic material (bioturbation, see Chapter 6), thus providing organic matter as food resources for saprophagous and/or microphytophagous animals in deeper strata of the soil. This vertical distribution pattern is modified by seasonal (and diurnal) migrations. Vertical distributions of Enchytraeidae, Acarina, Collembola, and larvae of Diptera are presented in Fig. 14.2.

### Temporal patterns

It is difficult to detect differences in seasonality between the soil and litter animal populations in mull and mor forests. In GÖ, the soil normally becomes rather dry during summer, particularly in July and August, which may lead to a phase of

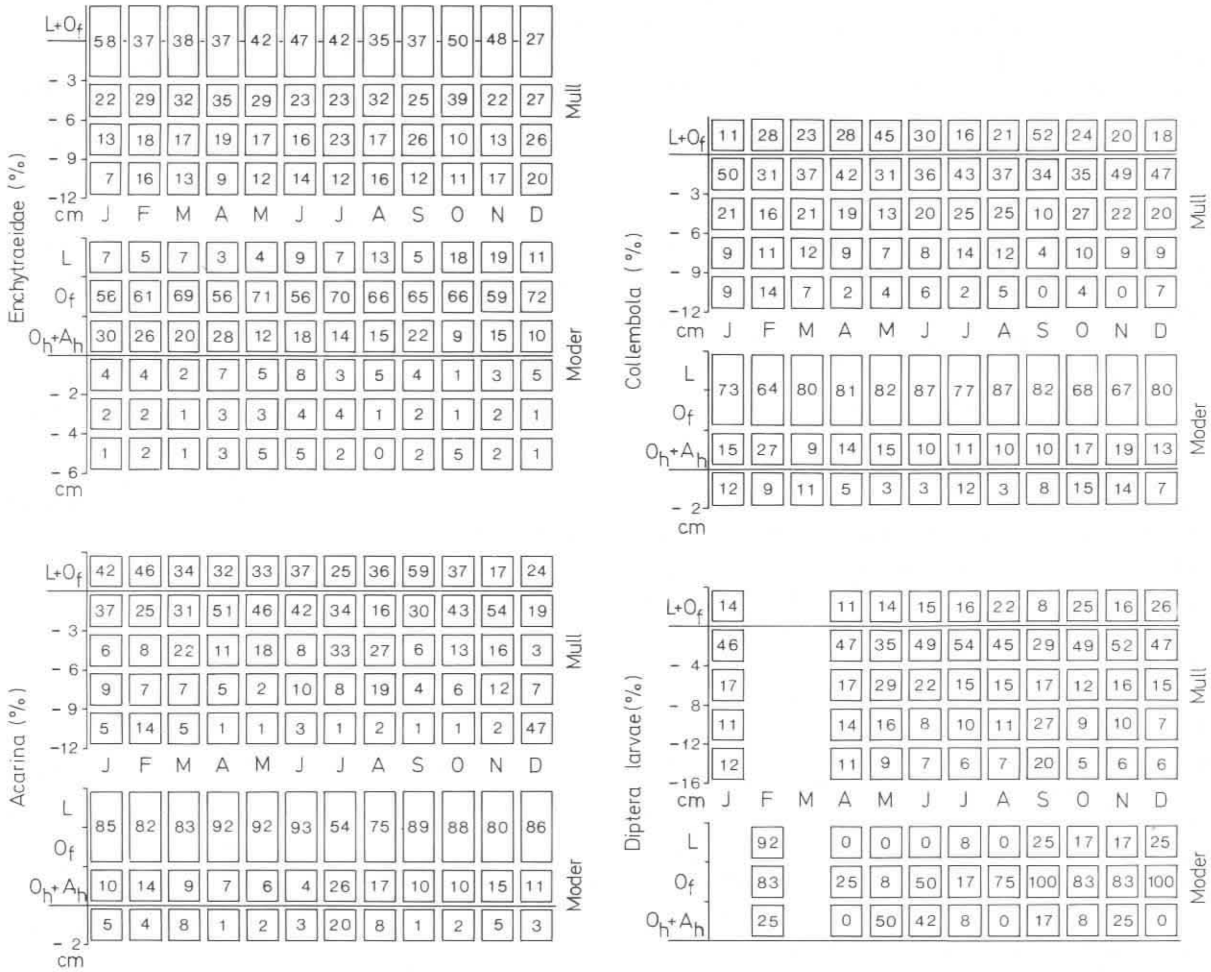


Fig. 14.2. Vertical distribution of Enchytraeidae, Acarina, Collembola and larvae of Diptera in beech-woods on mull soil (Göttinger Wald) and on moder soil (Solling). Data for Enchytraeidae (mull) from V. Büttner (pers. comm., 1986), for Acarina (mull) from H.-D. Baaske (pers. comm., 1986), for Collembola (mull) from Wolters (1983), for dipterous larvae (mull) from Hövemeyer (1984), data for the animal groups in moder soil from Schauermann (1986). Numbers for dipterous larvae in the moder soil indicate percentage of samples which contain dipterans.

inactivity or low population numbers of certain animal groups (Fig. 14.3). It appears from this Figure that the enchytraeid, acarine, collembolan and dipteran populations in SO have a peak during summer and autumn, a period which is not characterized by desiccation of the organic layers. High abundances of the soil fauna in winter are typical for SO, as compared to GÖ, probably because freezing of the soil may occur in mull profiles. Subzero temperatures rarely occur in moder or mor profiles, because the thick organic topsoil serves as an insulation layer during periods without snow.

## Food relations

In mor and moder soils leaf litter, partly decomposed litter, and fungal material are more abundant resources than in mull soils. Hence there are indications that moder and mor soils contain generally more fungivores, in particular among Collembola and oribatid mites, than mull soils (Wallwork, 1976).

Piearce (1972) observed that the earthworms in acid soils are predominantly litter-feeding, because calcium is available in the litter layer. Substrate-feeding species are favoured in mull soils, which have an $A_h$ horizon rich in organic material.

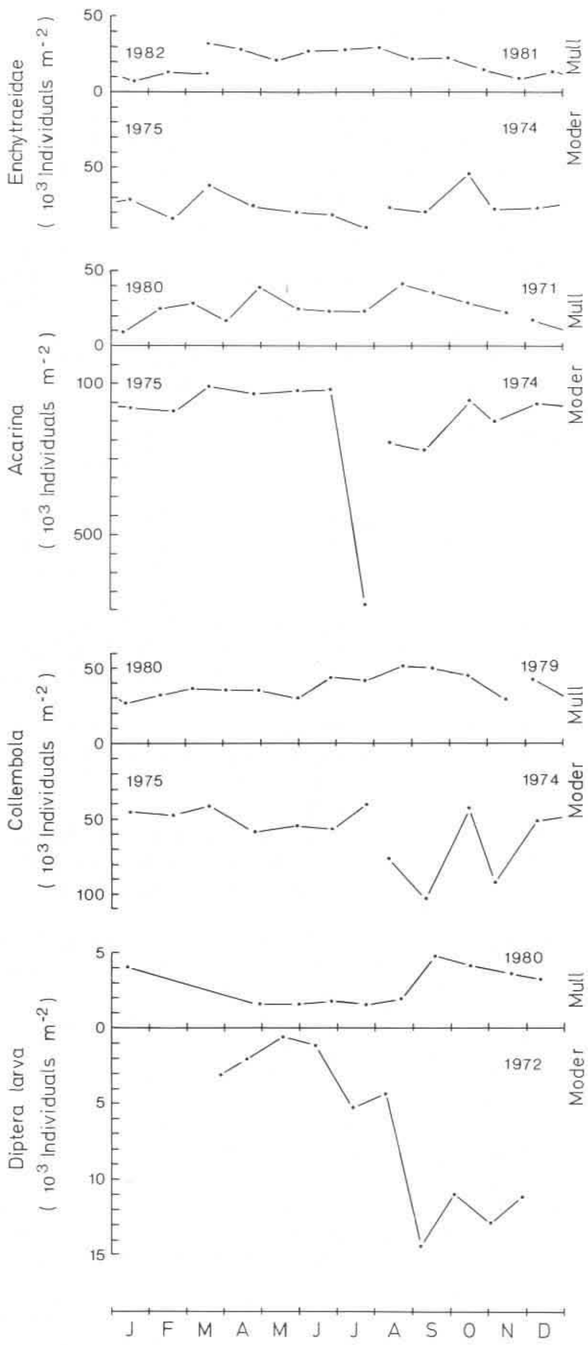


Fig. 14.3. Phenology of Enchytraeidae, Acarina, Collembola and larvae of Diptera in beech-woods on mull soil (Göttinger Wald) and on moder soil (Solling). Data for Enchytraeidae (mull) from V. Büttner (pers. comm., 1986), for Acarina (mull) from H.-D. Baaske (pers. comm., 1986), for Collembola (mull) from Wolters (1983), for dipterous larvae (mull) from Hövemeyer (1984), data for the animal groups in moder soil from Schauermann (1986).

## Summary


Petersen and Luxton (1982) have summarized the characteristics of the soil fauna in mull and mor soils of temperate deciduous forests. Several taxa, among them earthworms, are poorly represented in deciduous forests on mor soils. Estimates of total faunal biomass for Meerdink and SO are 5.2 g and 6 g dry wt $m^{-2}$ respectively. Biomass estimates for the soil fauna of mull soils range from 8 g dry wt $m^{-2}$ (HE) to a value of about 30 g dry wt $m^{-2}$ for a hornbeam (*Carpinus betulus*) forest at Brunoy (France). Thus mull soils are characterized by much higher total soil-fauna biomass than moder and mor soils. Mull soils are dominated by Lumbricidae, mor and moder soils by oribatid mites and Enchytraeidae. Generally, in temperate climates maximum faunal biomass is found in deciduous woodlands and grasslands on base-rich soils. Soil-fauna biomass appears to be temperature-limited in boreal latitudes, moisture-limited in arid zones, and food-limited by microbial competition in the tropics (Satchell, 1974; Swift et al., 1979).

Available data for mull and mor (moder) soils of temperate deciduous forests are summarized in Table 14.13.

The data presently available on forest ecosystems suggest an inverse relationship between weight of accumulated organic material on the soil surface and the total soil-fauna biomass (O'Neill and Reichle, 1979), which tentatively has been approximated by a negative power function (Petersen and Luxton, 1982). The input rate of litter as the primary nutrient source for the decomposer food web does not seem to be the most significant factor determining the biomass of the soil fauna. Faunal biomass is positively correlated with decomposition rate (see Chapter 9). The more rapid decomposition rate in mull soils appears to be determined by several factors: high lumbricid biomass, high biomass of other macrofaunal primary decomposers, and lower grazing pressure on fungal decomposers.


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